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A NEW *SCYTALOPUS* TAPACULO (RHINOCRYPTIDAE) FROM BOLIVIA, WITH NOTES ON OTHER BOLIVIAN MEMBERS OF THE GENUS AND THE *MAGELLANICUS* COMPLEX

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ABSTRACT.—In Bolivia in 1992 I tape-recorded and observed several individuals of an undescribed tapaculo of the systematically complex genus *Scytalopus* in humid-temperate forest near the city of La Paz. During March 1993, Bolivian colleagues and I collected a series of the undescribed taxon from two geographically distinct regions of Depto. La Paz, and confirmed its presence as far south as Prov. Chapare, Depto. Cochabamba. The new species, the Diademed Tapaculo (*Scytalopus schulenbergi*), is described and its distribution and vocalizations are compared with some other members of the genus, mostly in Bolivia. I reexamine systematics of the *magellanicus* group and, based primarily upon striking and consistent vocal differences across the North Peruvian Low in northwestern Peru, I recommend its division into two superspecies with the names *magellanicus* (southern populations) and *griseicollis* (northern populations). Received 22 July 1993, accepted 20 Feb. 1994.

The genus *Scytalopus* spans the entire range of the Andes (as well as the mountains of southern Central America and the mountains and isolated serras of eastern Brazil southward to Misiones, Argentina), and appears to have undergone a particularly complex speciation (Zimmer 1939; Fjeldså and Krabbe 1990; Arctander and Fjeldså, in press; T. Schulenberg and N. Krabbe, pers. comm.). That *Scytalopus* has not colonized pantepui probably reflects poor dispersal capability, a factor that has contributed to a rapid and diverse speciation in the geographically complex Andes. The informative accounts of *Scytalopus* taxa in Fjeldså and Krabbe (1990) represent the first comprehensive treatment of the genus in the Andes, and provide the first organized insight into the several species groups and multiple lower taxa involved (see Vielliard 1990 for a recent

treatment of Brazilian taxa). A great deal of confusion persists, however, and the relationships of many taxa remain obscure. The complexity of recognition of the various forms within *Scytalopus* is perceptually confounded by a general lack of understanding of the manner in which taxa segregate behaviorally and spatially. These complexities derive from several sources. First, *Scytalopus* inhabits an incredibly wide latitudinal and elevational distribution, with one or more members on virtually every slope of every cordillera, which inherently introduces limitations to the resolution of data because adequate collections from many Andean localities, even those relatively accessible ones, do not and may never exist. Secondly, *Scytalopus* displays only minor differentiation mensurally (Table 1) or in plumage, with many (all?) species showing age-related plumage variation (species may take several years to attain definitive plumage; Fjeldså and Krabbe 1990:422) that is usually greater than interspecific variation; its taxonomy is based upon types sometimes lacking reliable locality and/or elevational data, and always lacking vocal data, such that some existing names may be of dubious application to other specimens, especially those taken any distance from the type locality; additionally, *Scytalopus* comprises more species-level taxa than currently recognized, probably considerably more (Fjeldså and Krabbe 1990:422; Arctander and Fjeldså, in press; T. Schulenberg, N. Krabbe, and D. Stotz, pers. comm., pers. obs.); more than one species occurs at many localities, sometimes syntopically; and *Scytalopus* tapaculos are notoriously difficult to observe in the field owing to the dense understory vegetation frequented by most species, and the skulking nature of the birds; finally, because many of the species sing at long and unpredictable intervals, it is difficult to adequately tape-record full, unsolicited songs for comparative purposes.

Given these realities, the complexities of species limits in *Scytalopus* may be resolved in large measure when it is recognized that (1) at no known locality does more than one species of *Scytalopus* inhabit habitats above the natural local treeline (well away from the ecotone with the forest); (2) at the vast majority of localities, no more than two species of *Scytalopus* occur in the same habitat at the same elevation (this is especially true when the very large, possibly generically distinct *S. macropus* is considered separately); (3) bands of species overlap are narrow with respect to the width of the local elevational distribution of the species involved; (4) symmetrical white markings on the head are probably important plumage characters (T. Schulenberg and N. Krabbe, pers. comm.); and that (5) songs and scolds are highly stereotypical within local populations, and seem to be reliable indicators of taxonomic limits in this suboscine genus (Fjeldså and Krabbe 1990; Vielliard 1990; Arctander and Fjeldså, in press), although slight vocal differences (but often no plumage

TABLE 1
MEASUREMENTS OF SELECTED *SCYTALOPUS TAPACULOS*

Taxon	Culmen		Tarsus		Wing chord		Tail	
	N	\bar{x} (range)	N	\bar{x} (range)	N	\bar{x} (range)	N	\bar{x} (range)
<i>S. schulenbergi</i>	26	10.8 (10.2–12.1)	26	21.7 (20.4–22.7)	26	51.0 (47.1–55.0)	25	37.5 (33.8–43.2)
<i>S. argentifrons</i>	2	11.5 (11.4–11.6)	2	20.6 (20.6)	2	50.6 (49.3–52.0)	2	38.5 (37.9–39.1)
Unnamed (Cuzco, Peru)	2	10.7 (10.4–11.0)	2	22.2 (21.7–22.8)	2	50.0 (50.0–50.1)	2	33.5 (32.4–34.7)
Unnamed (Pasco, Peru)	12	11.3 (10.7–11.7)	12	20.2 (18.9–21.2)	12	52.2 (50.4–54.2)	12	36.5 (33.6–38.5)
<i>S. [m.] acutirostris simonsi</i>	11	11.3 (10.3–12.7)	12	20.2 (18.7–21.9)	12	50.0 (46.4–53.1)	12	36.3 (33.7–41.0)
<i>S. [u.] parvirostris</i>	12	11.1 (10.1–11.8)	12	22.2 (21.0–23.0)	12	51.6 (50.1–54.3)	12	38.7 (34.8–43.8)

divergence) within taxa may be observed across natural habitat breaks (pers. obs.).

Because plumage appears to be more conservative (and certainly more confusing) than voice, and because vocal differences appear to be correlated closely with genetic differences (Arctander and Fjeldså, in press), I suspect that species limits within *Scytalopus* will be settled as satisfactorily by the correlation of habitat, elevation, and the presence of certain recurrent geographic barriers with marked vocal shifts, as by any other approach. Molecular analyses will eventually allow a test of the vocal and morphological data to the extent that molecular material is accompanied by specimens that also have been tape-recorded.

In February 1992, while conducting an avifaunal survey in humid-temperate forest on the east slope of the Andes just over the pass from the capital city of La Paz, Bolivia, I heard, tape-recorded, and saw an apparently undescribed *Scytalopus* tapaculo. In March 1993, together with Omar Rocha O. of the Museo Nacional de Historia Natural in La Paz, I obtained a series of this form, and made further tape recordings documenting various of its vocalizations. Consideration of this tapaculo's distribution, vocalizations and, to a lesser extent, plumages, informed through examination of currently recognized species limits in the genus *Scytalopus* both in Bolivia and elsewhere in the Andes, convinces me that it is a new taxon best described as a new species, which I propose to name:

Scytalopus schulenbergi sp. nov.

DIADEMED TAPACULO

HOLOTYPE.—Colección Boliviana de Fauna (hereafter CBF) No. 2636; subadult male from about 4 km west of Chuspipata along the main road between La Paz and Coroico ("Cotapata" of Remsen 1985), 16°19'S, 67°51'W, 3215 m, Province of Nor Yungas, Department of La Paz, Bolivia; 28 March 1993; collected by Bret M. Whitney. Voice specimen archived at Library of Natural Sounds (hereafter LNS), Cornell Lab of Ornithology, Ithaca, New York; LNS No. 63427. Blood sample housed at Zoological Museum, Univ. of Copenhagen, Denmark (hereafter ZMUC).

DIAGNOSIS.—*Plumage*: A typical member of the genus *Scytalopus*, showing little sexual dimorphism and significant age-related plumage variation. Adults distinguished from most congeners, including the sympatric *S. [magellanicus] acutirostris* (see below for nomenclature) and *S. 'unicolor' parvirostris*, by silvery-white, transverse crescent on fore-crown (hereafter called "diadem"; Frontispiece, Fig. 1A; this and other photos to be archived at VIREO, Academy of Natural Sciences of Philadelphia). Adults are most similar to *S. argentifrons* of Costa Rica and western Panama, differing in more silvery-whitish throat, and duller and less extensive brownish color and absence of distinct dark spots and/or bars on the flanks and undertail coverts, and differ from other taxa having a diadem (unnamed taxon in Depto. Pasco, Peru; unnamed taxon in Depto. Cuzco, Peru) by the aforementioned characters, by generally darker coloration (which may, however, be due to



FIG. 1. Andes of extreme southern Peru south to central Bolivia, showing known localities for *Scytalopus schulenbergi*. 1. Valcón, Depto. Puno, Peru; 2. Pelechuco, Depto. Franz Tamayo, Bolivia; star, type locality (Cotapata), Depto. La Paz; 3. Prov. Chapare, Depto. Cochabamba. Broken line is Peru/Bolivia border. Dotted line is continental divide.

fading; see below), by longer tail (Table 1), and by absence of roughly concentric, alternating light and dark internal markings paralleling the margins of the rectrices. Adults further distinguished from *S. [m.] acutirostris* by the plain grayish tail (all ages of the latter show dark bars or other dark internal markings on the rectrices).

Juveniles are distinguished from *Scytalopus argentifrons* by generally paler coloration, and by much finer dark markings on individual feathers of head and body such as to appear barred throughout, lacking the scalloped pattern produced by wide, dark subapical lunules of *argentifrons*. They also appear to be distinguishable from *[m.] acutirostris* by dark subapical pattern of individual feathers of underparts: marked with a bar curving proximally to reach the feather margin in *schulenbergi*; marked with a wholly internal, teardrop-shaped band surrounding the feather shaft completely, enclosing a light-colored region along at least the distal portion of the shaft, in *[m.] acutirostris*. Differs from 'unicolor' *parvirostris* by grayer crown to upper back of that species, and by the same individual feather characteristics of *[m.] acutirostris* described above, only heightened in degree in 'unicolor' *parvirostris* by the greater width of these dark markings. Juveniles of *schulenbergi* having clearly barred central rectrices (as opposed to those marked with roughly concentric dark bands) may be distinguishable from both the latter two species by the presence of 7–8 thin dark bars as opposed to 3–5, relatively wider bars of the other two species. A larger sample will aid considerably in establishing the diagnosability of juvenal plumages.

DIAGNOSIS.—Voice: Full songs are distinguishable from those of all known congeners by the pattern of the first three or four seconds taken together with the overall duration of

the song (see sonagram figures). The scold and some other vocalizations are not 100% diagnosable.

DISTRIBUTION.—Known from as far north as Valcón, 14°16'S, 69°24'W, 3000 m, Department of Puno, Peru to as far south as approximately 16°30'S, 65°30'W, 3200 m, in the Province of Chapare, Department of Cochabamba, Bolivia, and two points in between: the type locality; and 5 km by trail east of Pelechuco, 14°48'S, 69°03'W, 3350 m, Province of Franz Tamayo, Department of La Paz (Fig. 2).

DESCRIPTION OF HOLOTYPE.—Forecrown marked by narrow (1.5 mm) frontlet of short, somewhat stiffened blackish feathers surrounding base of maxilla, bordered posteriorly by a partial, white diadem, the feathers of which are in obvious molt, widest on centerline of crown, and tapering laterally and posteriorly to a point above and behind eye, terminating approximately 2 mm behind posterior edge of orbit (Frontispiece, Fig. 1A). Diadem feathers with a reflective quality such that contrast and extent of diadem are seen to change relative to viewing angle. Diadem appears deepest (about 6 mm) and brightest from a superior, frontal angle, and narrowest and duller when viewed from directly above or slightly behind. Crown posterior to diadem near Blackish Neutral Gray (capitalized color names from Smithe 1975). Lores same blackish color as narrow frontlet, this blackish extending posteriorly to narrowly surround eye. Nape and entire dorsal surface washed lightly with dull brown, most heavily along centerline of back and continuing to the rump. Scapular region more nearly approaches Blackish Neutral Gray color of crown. Chin and throat to a point approximately 7 mm posterior to base of mandible, silvery-gray with a reflective quality, grayer than diadem and, when viewed from the front, contrasting with blackish sides of head and, to a lesser extent, rest of underparts. Throat, when viewed from lateral or posterior perspective, appears close to Medium Neutral Gray, and contrasts less with dark feathering of the face and remainder of underparts. Underparts from base of throat to lower belly and including sides of breast and sides, near Dark Neutral Gray, displaying a silvery, graphite-like sheen on the feather margins, palest on the lower belly. Flanks and undertail coverts unmarked dull orange-rufous anteriorly, becoming weakly but increasingly barred posteriorly, the pattern of each feather consisting of two dark gray subapical bars, the most proximal of which sometimes surrounds the feather shaft blending into the dark gray base of the feather. Feathers of flanks, and especially those of lower back, much elongated (to 27 mm), loosely integrated, and somewhat downy in composition. Rump same dull orange-rufous as flanks and undertail coverts and similarly barred; uppertail coverts grayer with a weak orangish tinge, especially basally, and a hint of the barred pattern seen on the rump. Tail near Blackish Neutral Gray with a faint brownish cast. Rectrices lacking any pattern of barring or internal marking, but each having a minute brownish fringe anterior to tip. Wings, including all coverts, also Blackish Neutral Gray except two innermost tertials, which are mostly dull brownish with one subapical, dark gray bar on distal web. Other remiges with a narrow brownish fringe on proximal portion of distal web, imparting a weak brownish cast to folded wing. Soft parts in life: iris dark brown; tarsi and feet dark yellowish-brown; maxilla black; mandible dark brownish-black, slightly paler at base. Although it is not the best plumage example available (being a subadult in heavy molt), CBF No. 2636 was selected for the holotype because it was tape-recorded and a blood sample was obtained.

MEASUREMENTS OF HOLOTYPE.—Wing (chord) 48.9 mm; tail 38.3 mm; culmen from base (at skull) 10.3 mm; tarsus 20.4 mm; weight 15.2 g.

DESCRIPTION OF FEMALE.—The following is based upon paratype, CBF No. 2629. Similar to holotype. Differs from adult male by diadem both duller and reduced in the center, and by somewhat duller silvery throat. Upperparts entirely dingy brownish-gray, brownest in nuchal region. Uppertail coverts, flanks, and undertail coverts dull brownish



FIG. 2. A. Adult male *Scytalopus schulenbergi*, showing silvery-white diadem, pale throat, and blackish mask. B. Dense, somewhat stunted humid-temperate forest at 3300 m along the Rio Pelechuco in northern Bolivia, habitat of *S. schulenbergi*. *S. [magellanicus] acutirostris* replaces *schulenbergi* above treeline in rocky shrub/grassland, visible here on the upper slopes of the valley.

marked with two or three inconspicuous dark gray bars. Remiges with slight brownish tinge, especially toward margins. Soft parts as in males.

DESCRIPTION OF JUVENILE.—No indication of diadem or mask. Generally golden-brown, darker dorsally than ventrally, and reflective sheen on feathers obsolete. Every feather of head and body with a conspicuous dark subapical marking, over almost the entire upperparts, face, throat and upper breast in the form of a single, small Dark Neutral Gray spot at the most distal furcation of barbs on the feather shaft, but scapulars marked with a short streak along the shaft. Through remainder of underparts, subapical spot broadening and thickening slightly to become a bar. Elongated flank feathers, belly, and undertail covert feathers each marked with two or three bars that curve slightly proximally toward feather margin, producing a weakly lunulated pattern, most pronounced on belly. Tail dark golden-brown, each rectrix with seven or eight narrow, transverse bars or, apparently more rarely, two or three roughly concentric internal bands. Wing coverts with dark markings expanded greatly to cover proximal web of each feather to tip, leaving a relatively bright, golden-brown crescent at tip of distal web, coverts together forming fairly conspicuous, black-bordered wing-bars, most pronounced on greater primary coverts. Remiges near Dark Neutral Gray edged golden-brown, with margins soft and barbs weakly integrated; some individuals show light and dark spots on the distal webs of the outer primaries. Each tertial with a conspicuous subterminal bar curving proximally inside feather margin, and expanding to feather tip in a narrow point along shaft, producing, in effect, a series of black-bordered, pale crescents overlying folded wings. Soft parts as in adults, except legs decidedly yellowish.

SKIN SPECIMENS EXAMINED.—*S. schulenbergi*: Peru: Puno, Valcón, 6 ♂♂ and 3 ♀♀ (Louisiana State Univ. Museum of Natural Science [hereafter LSUMNS] No. 98394, 98395, 98396, 98399, 98400, 98401, 98402, 98406, 98407); Bolivia: La Paz, Prov. Franz Tamayo, 1 ♂ and 1 sex unknown (CBF No. 2640, 2641); La Paz, Prov. Nor Yungas, 8 ♂♂, 3 ♀♀, 3 sex unknown (CBF No. 2624–2630, 2632, 2633, 2636, 2637; LSUMNS No. 96092, 102258, 102261), and 1 sex unknown in alcohol (CBF No. 2631); Cochabamba, Prov. Chapare, 2 sex unknown juveniles (LSUMNS No. 37776, 37780). *S. argentifrons*: Costa Rica, Prov. San José, 1 ♂; Prov. Cartago, 2 ♂♂; Prov. Heredia, 1 ♀ (LSUMNS No. 62660, 135543, 135544, 138717). *Unnamed taxon*: Peru: Pasco, various localities near Depto. Huanuco border (Marín, Millpo, Abra Portachuelo), 16 ♂♂ and 2 ♀♀ (LSUMNS No. 128613–128629; Museo de Historia Natural Javier Prado, Lima, Peru No. 7333); Huanuco, within 2 km of Depto. Pasco border, 3 ♂♂ and 2 ♀♀ (LSUMNS No. 128608–128612). *Unnamed taxon*: Cuzco, 14 km NE Abra Málaga, 1 ♂ and 1 ♀ (LSUMNS No. 78579, 78580). *S. [magellanicus] acutirostris*: Peru: Puno, Valcón, 2 ♂♂ and 3 ♀♀ (LSUMNS No. 98397, 98398, 98403, 98404, 98405). Bolivia: La Paz, Prov. Franz Tamayo, 1 ♂ and 1 ♀ (CBF No. 2642, 2644); La Paz, Prov. Nor Yungas, 1 ♂, 1 ♀, and 1 sex unknown (CBF No. 2634; LSUMNS No. 90751, 96091); Cochabamba, Prov. Chapare, 2 ♂♂ and 1 sex unknown (LSUMNS No. 36130, 37775, 37779); Prov. Arani, 2 ♂♂ (LSUMNS No. 124233, 124234). *S. [m.] superciliaris zimmerlacutirostris* intergrade(?): Bolivia: Cochabamba, Colomi, 1 ♀ (LSUMNS No. 37781). *S. [m.] magellanicus*: Argentina: Rio Negro, 2 ♂♂ and 1 ♀ (LSUMNS No. 25099, 25100, 70003). *S. 'unicolor' parvirostris*: Bolivia: Prov. Franz Tamayo, 1 ♀ (CBF No. 2646; probably not true *parvirostris*, see below); La Paz, Prov. Nor Yungas, 5 ♂♂, 3 ♀♀, and 2 sex unknown (CBF No. 2635; LSUMNS No. 90750, 102254, 102255, 102256, 102257, 102259, 102260, 102262, 102263); Cochabamba, Prov. Chapare, 1 ♂ and 1 sex unknown (LSUMNS No. 36133, 37778). *S. 'femoralis' bolivianus*: Peru, Puno, Abra de Maruncunca, 1 ♂ (LSUMNS No. 98393); Bolivia: La Paz, Serrania de Bellavista, 1 ♂ (LSUMNS No. 90749); La Paz, Prov. B. Saavedra, 2 ♂♂ and 1 ♀ (LSUMNS

uncataloged specimens from 1993); Sana Cruz, Samaipata, 1 sex unknown (LSUMNS No. 37773).

VOICE SPECIMENS EXAMINED.—All recordings made by the author unless otherwise indicated. *S. schulenbergi*: Bolivia: La Paz, 27 (representing more than 30 individuals, including CBF No. 2624, 2625, 2633 [juv scolds], 2636 [LNS No. 63427], 2640 [juv songs], and 2641); Cochabamba, 2 (representing probably 3 individuals). *S. argentifrons*: Costa Rica: Puntarenas, 3; Panama: Chiriqui, 2. *Unnamed taxon*: Peru: Pasco, 3 (including LSUMNS No. 128629; 3 G. Rosenberg). *S. [magellanicus] acutirostris*: Peru: Cuzco, 2 (representing 3 individuals); Bolivia: La Paz, 10 (representing 9 individuals, including CBF No. 2634 and 2644); Cochabamba, 9 (representing 6 individuals; 1 R. A. Rowlett); *S. [m.] superciliaris*: Argentina: Tucumán, 2 (representing 3 individuals; 1 D. Stejskal); *S. [m.] fuscus*: Chile: Santiago, 2 (1 G. Egli); *S. [m.] magellanicus*: Argentina: Tierra del Fuego, 2 (1 J. Arvin); Chile: Malleco, 2. *S. 'unicolor' parvirostris*: Bolivia: La Paz, 3 (including CBF No. 2635); Cochabamba, 3; Santa Cruz, 5. *S. 'femoralis' bolivianus*: Bolivia: La Paz, 2 (representing 1 individual); Cochabamba, 3 (1 R. A. Rowlett). All recordings made by the author have been or will be archived at LNS. All recordings of collected birds will also be archived at the respective institutions where the skins are held.

BIOCHEMICAL SPECIMENS.—*S. schulenbergi*: Peru: Puno, two tissues (LSUMNS No. B-501 and B-522); Bolivia: Franz Tamayo, two blood samples (CBF No. 2640 and 2641); La Paz, two blood samples (CBF No. 2636 and 2637). Blood samples stored in APS buffer at ZMUC.

ETYMOLOGY.—I am pleased to name this new tapaculo after my friend and colleague Thomas S. Schulenberg, whose field work and informed insights have, for more than a decade, greatly aided many investigators in pursuit of knowledge of Andean birds. In 1980, he headed the LSUMNS expedition into the remote area of Valcón in Puno, Peru, that brought back a fine series of the new species. Finally, it was Tom who several years ago first encouraged me to delve into the depths of *Scytalopus*.

The proposed English name, Diademed Tapaculo, refers to the shining-white, crescent-shaped band marking the forecrown of adults of the new species, which occurs predominantly in Bolivia. Should the similarly "diademed" (but presently unnamed) tapaculo inhabiting the Abra Málaga region of central Peru (see below) eventually prove to be related to but specifically distinct from *schulenbergi*, I suggest the names Bolivian Diademed Tapaculo for *S. schulenbergi*, and Peruvian Diademed Tapaculo for the Abra Málaga bird.

REMARKS

Variation in the type series.—I restrict the type series to those (10) specimens collected at the type locality in 1993. This limitation ensures that the series contains truly comparable material, eliminating variation introduced by such factors as age of the prepared specimens, which may be significant (see below). Among males, the most consistent variation from the holotype is seen in the flanks and undertail coverts, which are washed more extensively and brightly with dull orangish-brown on some specimens, more weakly on others, but with barring, ranging from very weak to well-defined, present on all except one. This latter specimen (CBF No. 2632) is probably an adult in definitive plumage, and shows only a very weak tinge of brownish in the flanks and undertail coverts, and no trace of barring. The most conspicuous variation among males,

however, is seen in the extent and brightness of the diadem. In relation to the holotype, four have a more extensive diadem (two of these having diadems covering almost the entire front half of the crown), and two have reduced and significantly duller diadems, more similar to that of the holotype. Otherwise, males vary little from the holotype except that some are washed more extensively with dull brownish through the upperparts, concentrated on the lower back and rump. These specimens also show the most color and barring on the flanks and undertail coverts, and include the specimens with the smallest and dullest diadems. These birds, like the holotype, are probably subadults.

The series contains two specimens that are unequivocally in subadult and juvenal plumages, respectively; the latter is described above. The subadult (CBF No. 2627, sex unknown) was in molt of the head and body but not the wing or tail. The head, which was largely destroyed by shot, is generally brownish, with the center of the crown slightly grayer and a faint indication of a silvery diadem. The upperparts are as in the juvenal plumage, but the feathers of the neck, throat, and breast have been replaced with feathers of Medium Neutral Gray, the lower of which have narrow buff fringes. Additionally, some of the large, dull orangish-brown feathers of the lower sides (flanks?) are marked with two bars that curve proximally inside the feather margin to form a pattern distinct from that of juveniles or adults. The wing feathers appear to be newly replaced, but the tail is somewhat abraded and is likely the juvenal plumage. The wing-coverts are brownish-gray, except for a golden fringe and dark subapical spot on the distal web of each of the greater primary coverts, producing a faint wing-bar. The remiges lack the weakly integrated fringes and the light-spotted pattern on the edges of the distal webs of the juvenal remiges but are overall somewhat browner than those of older birds. This individual was not tape-recorded, but I heard it give a single loud "tek!" note that I have definitely associated with *S. schulenbergi*. As a final note, one specimen (CBF No. 2630) shows a single white feather on the side of the neck. Asymmetrical albinism of this nature is fairly frequent among *Scytalopus* (N. Krabbe and T. Schulenberg, pers. comm.).

Variation among the 18 additional specimens of *S. schulenbergi* examined is similar to that observed in the type series. In comparison with specimens from the type locality, those from Puno, Peru, and Prov. Franz Tamayo, Bolivia, may have slightly reduced diadems. The single juvenile from Franz Tamayo has a distinctly buffier throat than the one from the type locality. Among the predominantly gray-bodied *S. schulenbergi* examined, there is a consistent difference in general coloration between the birds collected in 1993 (nine; eight from the type locality, and one from

Franz Tamayo) and those collected in 1980 and 1981 (11; two from the type locality and nine from Puno, Peru). The more recent specimens are darker throughout, especially in the underparts, which are near Dark Neutral Gray, whereas the older specimens are all closer to Medium Neutral Gray through the underparts. Furthermore, the flanks and undertail coverts of the older specimens are lighter in color, more orangish and less brownish. These apparent differences are of the order of magnitude considered by Zimmer (1939) to warrant subspecific recognition. Because of the overlap of the localities involved, however, I have no doubt that these differences are due to the age of the specimens ("foxing").

Breeding and molt.—None of the specimens collected in March was in breeding condition (largest testis measured 5×2.5 mm). Gonads of most specimens were described as "little developed" (O. Rocha O. on specimen labels). We did encounter several juvenile *S. schulenbergi*, the plumage of which was advanced only a little beyond full juvenal, suggesting that they had fledged recently (although it is not known how long this plumage is retained or whether there is intraspecific variation in timing of the onset of post-juvinal molt). Judging from the few specimens available, the post-juvinal molt commences with the feathers of the head, throat, and breast, and it is probably this molt that produces the earliest indications of the silvery diadem (as discussed earlier with respect to subadult plumage). Aside from the juveniles, all March specimens showed conspicuous molt of some part of the plumage, and most birds in adult or near-adult plumages were in extensive molt of the entire plumage. Except for a few songs given early in the morning, *S. schulenbergi* was singing very little in late February and March (especially little on rainy days), less than I would expect if the birds were actively engaged in territorial activities. None of three La Paz *S. schulenbergi* collected 1 June, 31 July, and 4 August is in breeding condition; data on molt are lacking. The series of nine birds from Puno, Peru, taken in October may be considered to be in breeding condition, with testes ranging in size from 7×4 to 10×4 mm, and ovaries well developed. One female was observed "bringing food to nest." This nest and the two nestlings it held were collected (T. Schulenberg, pers. comm.; LSUMNS Egg and Nest Collection No. 907), and the nest was described as that of *Scytalopus magellanicus* by Rosenberg (1986). No data on vocalizations or molt were recorded on the Puno specimen labels. These considerations suggest that breeding takes place primarily between September and January, although data are lacking (aside from one specimen) for the period April to August.

Habitat and ecology.—*Scytalopus schulenbergi* lives only inside and at the edge of humid-temperate "cloud forest" and "elfin" forest and is so far known only from the east slope of the Andes. It does not occur in

habitats above the local treeline (whether natural or man-altered), although I expect that individuals wander a short distance out of the forest proper into the shrubby forest/grassland ecotone. All of the four known localities of occurrence are characterized by steep, forested slopes at or near treeline (Fig. 1B).

Remsen (1985) provided an excellent description of the habitat at the type locality of *S. schulenbergi* near Chuspipata, La Paz. His account covered two somewhat different sites about 5 km apart, one at 3050 m (Chuspipata) and the other at 3300 m (Cotapata). *S. schulenbergi* is common at both sites, but is especially common, and the only *Scytalopus* present, at Cotapata (the type locality). As noted by Remsen (1985), *Chusquea* sp. bamboo is abundant in the area, especially at Chuspipata, where the forest is more heavily disturbed by both natural landslides and selective logging (pers. obs.). *S. schulenbergi* does not appear to inhabit patches of *Chusquea* preferentially over areas of the understory dominated by other plants. It does seem to be partial to small ravines, perhaps especially those with a seepage of water, and bamboo is often dominant at such sites. The habitat description provided by Remsen (1985) applies closely to the other known localities of occurrence of *S. schulenbergi* in Bolivia, except that the site below Pelechuco in Prov. Franz Tamayo has suffered considerably more forest disturbance through cutting for firewood and fragmentation for garden space. *S. schulenbergi* appears to be much less common at this site.

The elevational range of *S. schulenbergi*, which is between about 2975 and 3400 m, overlaps that of two congeners, one at either extreme. *S. [m.] acutirostris* occurs primarily in the shrub/grassland above treeline (whether natural or not) but extends as low as the local limit of forest, penetrating the forest border wherever connected grassy or rocky openings permit. Thus it occurs alongside *schulenbergi* throughout the range of the latter (documented with specimens and tape at all known localities for *schulenbergi*), and the two can often be heard from the same position near the grassland/forest ecotone. It is the habitat more than the absolute elevation that determines the local elevational limits of these two taxa (e.g., north- and south-facing slopes of a wide canyon often have the natural grassland/forest ecotone at significantly different elevations; this ecotone around "treeline" in the Andes has been altered extensively by man). In the vicinity of Chuspipata, La Paz, *S. 'unicolor' parvirostris* reaches its upper elevational limit at approximately 3100 m and is common as high as just over 3000 m. In the narrow band between about 2975 and 3100 m, it occupies the same habitat as *schulenbergi* and on occasion the two can be heard in exactly the same place. It appears that the slightly larger *parvirostris* (Table 1) is the dominant or more aggressive of the

two, because playback of *schulenbergi* songs or scolds within the overlap zone were (in late March, at least) more likely to elicit a response from *parvirostris* than *schulenbergi*, but playback of *parvirostris* vocalizations elicited response only from *parvirostris*. This may have as much to do with the species' respective (and largely unknown) breeding seasons as anything else. The only other insectivore that forages primarily on or very near the ground within the latitudinal and elevational distribution of *S. schulenbergi* is the Rufous Antpitta (*Grallaria rufula*) (Formicariidae), which has a considerably larger body mass. The Stripe-headed Finch (*Atlapetes torquatus*) barely overlaps *S. schulenbergi* at the lowest elevations (Remsen 1985; pers. obs.)

Foraging and other behaviors.—*S. schulenbergi*, like all members of the genus, was quite difficult to observe in an undisturbed foraging routine; for most individuals, I managed to make only general, brief (less than 5 sec) foraging observations. The following information comes from a single adult that at first had been scolding me but which I subsequently kept more-or-less in view for about 10 min as it unconcernedly foraged around me in a relatively open place in the undergrowth. This bird remained within about 50 cm of the ground the entire time, almost always within about 20 cm, and came down onto the ground several times. It moved slowly with very short hops, perching briefly on both horizontal and (less often) vertical perches, holding its tail at a relaxed angle (not cocked), and stopping briefly to scan the surrounding mossy ground, branches, and vegetation. It occasionally reached to and gleaned from these substrates (terminology follows Remsen and Robinson 1990) and also probed the moss coating thin vertical trunks and dead branches, usually spending less than 3 sec at such a site. While on the ground, the bird performed the above maneuvers and seemed to explore the upper few mm of the leaf litter visually and with light probes. It did not scratch or otherwise manipulate the leaf-litter or moss with its feet and did not reach to vegetation significantly overhead (such as the undersides of leaves). While I was standing on the trail after observing the above behaviors, the bird again appeared, hopping out into the middle of the 1.5 m-wide trail, where it froze with the tail cocked sharply over the back, then fluttered weakly up to the edge of a 2.5 m-high bank and resumed foraging somewhat more actively on mossy limbs about 30 cm above ground (from which position it could keep an eye on me below). No other birds were seen in the vicinity during these observations. The bird's white diadem was conspicuous as it moved through the dark understory, which may help members of a pair to keep in visual contact without vocalizing.

Three *S. schulenbergi* specimen labels indicate that the stomachs contained insects; no other stomach contents were recorded. The 14 stomachs

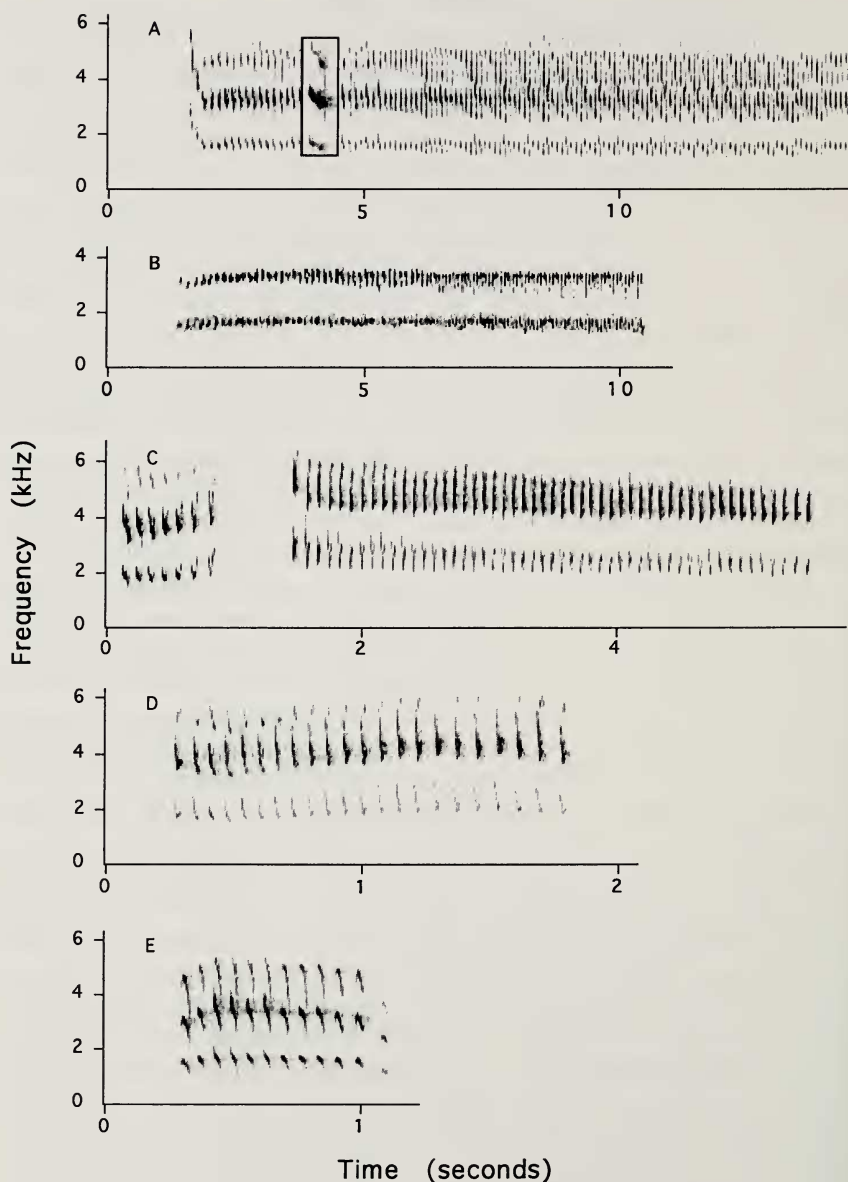


FIG. 3. Some vocalizations of *Scytalopus schulenbergi* from type locality for comparison with those of other taxa shown in subsequent figures. A. Adult male, song after playback, but one of natural variants; first 12.7 sec of 13.5 sec song (length variable); first one or two, burry syllables missed, end same as part shown. Noticeable 6-syllable pattern beginning at 6-sec point (repeated slants down to right) is not audible, and probably represents the bird's

collected in March 1993 have been preserved in alcohol at CBF, but have not yet been analyzed.

S. schulenbergi sings from a perch between about 20 cm and 3 m above ground on a horizontal limb, holding the head up and the tail pointing mostly toward the ground but not straight down. The throat is puffed out somewhat and the bill is opened only slightly. After playback of songs, males usually approached the tape recorder within 3 min, and in a couple of instances, climbed to as high as about 7 m above ground before singing in response. On several occasions, males appeared after tape playback, but did not vocalize. The single female collected in March responded to tape playback of its own scolds (Fig. 3D, E).

Were it not for its conspicuous voice and predictable response to tape playback, *S. schulenbergi* would be very difficult to detect and capture. In 17,587 daylight net-h (and an equal number of nighttime hours) at two sites in the humid-temperate forest near Chuspipata, La Paz (Remsen 1985), where *schulenbergi* is one of the most common birds in the forest undergrowth along roads and trails (pers. obs.), only two individuals were captured, and several hundred man-h (mostly without tape recorders) produced only one specimen shot. This is certainly understandable, considering the skulking nature of *Scytalopus* tapaculos in general, their reluctance to fly even short distances, and their generally slow progression through the undergrowth as they forage independently with near-perch maneuvers, allowing them to detect a mist-net the first time it is encountered (after the first encounter, entanglement in the net is probably very unlikely). Capture of the single specimen we netted required careful net-site selection and the practiced use of a tape recorder. Even then, the bird obviously avoided the net on the first pass and later became lightly entangled only in the lowest part of the net, the bottom several cm of which we had arranged on the ground, when it attempted to crawl under it. As the behavior of *schulenbergi* does not appear to differ significantly from

←

breathing interval (recording made at ideal level, 5 m range, at 15 i.p.s.); 3380 m, 02 Mar 1993; CBF 2624. Inset in song of this and other figures represents an individual note/phrase (bisyllabic in some taxa) enlarged on time scale (same scale for all figures) to show more comparative detail. B. Age/sex unknown, complete natural song, with slow first half (and low beginning) and rapid second half; bird distant from microphone. 3100 m, 24 Feb 1992. C. Subadult, complete descending-series song, with sharp, rising-series introduction; after playback. 3190 m, 28 Mar 1993; CBF 2637. D. Adult female, excited scold soon after playback. E. Same adult female, scold typical of species, given by both sexes and all ages. 3395 m, 02 Mar 1993; CBF 2629. Sonagrams produced with "SoundEdit" of Farallon Computing, Inc., Emeryville, California, and "Canary" of the Bioacoustics Research Program at the Cornell Lab of Ornithology, Ithaca, New York.

that of forest-based congeners (pers. obs., although it may prove to be somewhat more arboreal, and it seems easier to see with tape playback than most), it is easy to imagine that avifaunal surveys (especially brief ones) that have not used tape recorders routinely could have missed some of these forest-based *Scytalopus* and possibly some of the taxa above treeline as well.

Vocalizations.—Almost all of the vocalizations of *S. schulenbergi* are distinctive and may be used to diagnose it from congeners more reliably than its various plumages. The primary song is a level series (sometimes dropping or rising slightly through the first few syllables) of very closely spaced syllables at about 3.3 kHz, lasting between about 7–15 sec, averaging about 9 sec. The song begins with 4–5 slightly burry or throaty syllables spaced far enough apart to be counted easily, after which it accelerates steadily for several seconds, either continuing at an even rate to the end of the song (Fig. 3A; first couple of notes missed) or sometimes abruptly accelerating once again in the final half (Fig. 3B). Songs delivered in response to tape playback are often considerably longer (up to 48 sec) and usually have scattered stutters in the series. This song apparently is given by individuals of any age, judging from a juvenile that was tape-recorded delivering it (albeit in response to playback) and collected (CBF No. 2640; sex unknown). I do not know whether females sing, but my observations suggest that they do not. A second song-type is a rapidly delivered, steadily descending series lasting 3–5 sec, often preceded by either a few loud, hard “tek!” syllables spaced 1–2 sec apart or, especially after tape playback, a rapid, sharp, rising series of syllables lasting about 0.5 sec (Fig. 3C). I suspect that this vocalization is given only by subadult birds, perhaps those less than one year old. Each instance in which I was able to see the bird that had definitely given this descending series, it proved to be either a juvenile or a bird in a plumage not far advanced from the juvenal ($N = 6$, 1 collected [CBF No. 2637]). To my knowledge, such noticeable age-related variation in the song has not been reported among suboscines (in fact, the contrary is the norm); I wish merely to report the possibility of its involvement in this case. In any event, I believe that this descending series is indeed a song in the sense that songs have been described in the genus, as it is delivered only once, at long intervals, from a perch above ground, and in the singing posture described above. All these songs differ appreciably from those of other *Scytalopus* taxa (compare Fig. 3A–C with Fig. 4A–C, Fig. 5A, and Fig. 6A), especially the sympatric *S. [m.] acutirostris* and *S. ‘unicolor’ parvirostris*.

S. schulenbergi also frequently gives a scold or mobbing vocalization, heard most often when an individual is startled or disturbed by an observer, or in response to tape playback. A bout of scolding/mobbing may

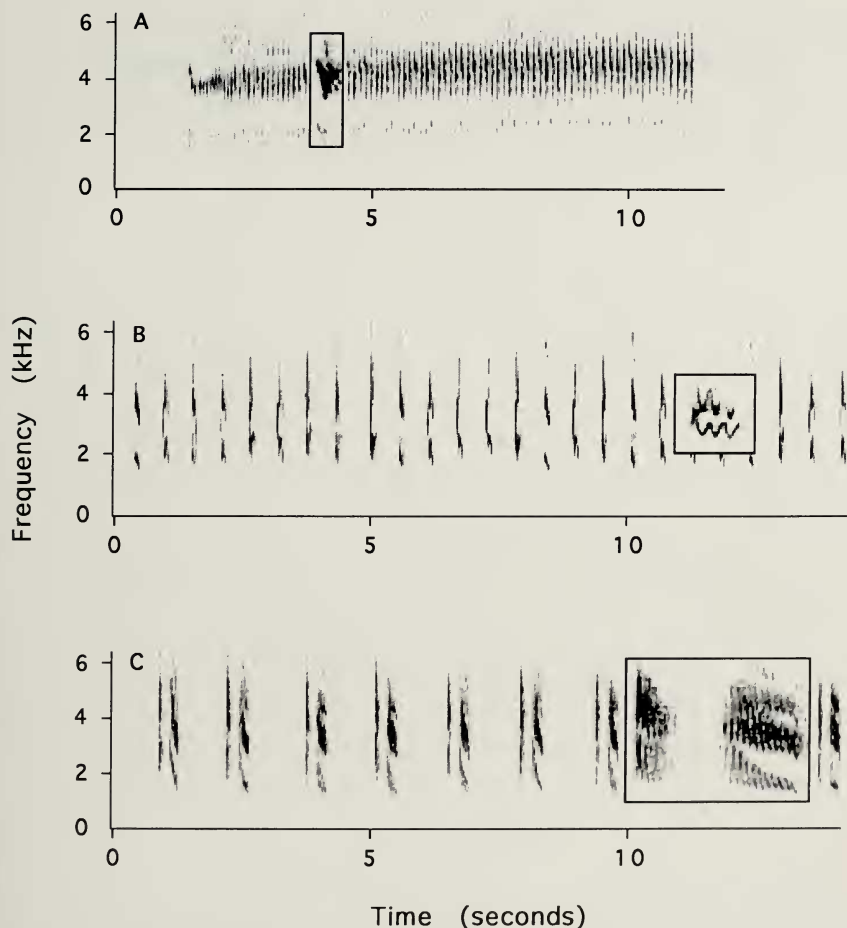


FIG. 4. Songs of other diademed/white-browed *Scytalopus*. A. *S. argentifrons*: age/sex unknown (male?), complete natural song. Costa Rica, Prov. Puntarenas, Monteverde Cloud Forest Preserve, 1600 m, 24 Mar 1983. B. Unnamed taxon: Adult male, natural(?) song; section of series of 45 continuous chirping notes; another series of 107 continuous notes also recorded; apparently neither was a truly complete series. Peru, Depto. Pasco, Millpo, approx. 3700 m, 29 July 1985; LSUMNS 128629; recorded by G. Rosenberg. C. *S. superciliaris* Adult male(?), section of song after playback, same as natural; length of series highly variable, from 27 notes, to 132 in 3:10 sec during a countersinging bout. Argentina, Prov. Tucumán, 13 km by road W Tafi del Valle, 2730 m, 20 Oct 1989.

last several minutes and often attracts other species of birds which may begin giving analogous vocalizations. When giving this vocalization, attention is directed at the observer, although the bird usually remains largely hidden from view. Individuals of all ages and both sexes of *S. schu-*

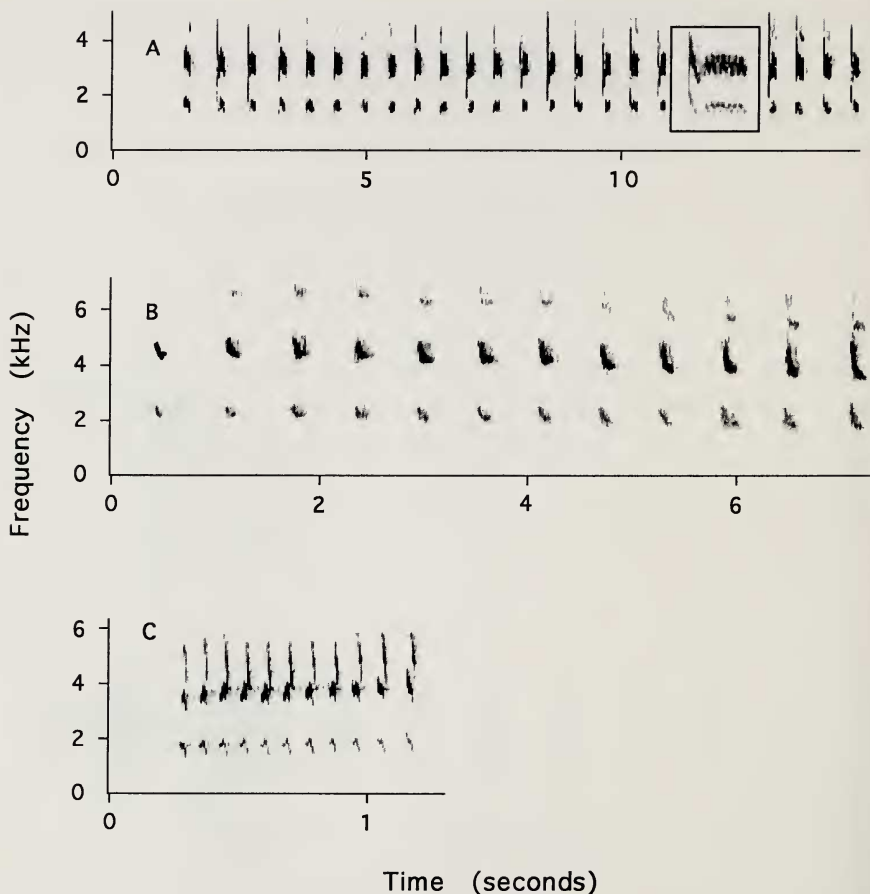


FIG. 5. Some vocalizations of *Scytalopus [magellanicus] acutirostris*. A. Adult (male ?), section of song after playback, same as natural. This song comprised 85 weakly bisyllabic notes, and lasted 50 sec. Depto. Cochabamba, Prov. Quillacollo, slopes of Cerro Tunari above Quillacollo, 3275 m, 14 Mar 1993. B. Subadult (age/sex unknown), natural descending series; number of notes variable from 4–12, often given by presumed female while male is singing. Same loc., 3400 m, 26 Feb 1992. C. Age/sex unknown, natural scold; this voc. not yet documented from Cochabamba populations. Depto. La Paz, Pongo, about 3615 m, 24 Mar 1992.

lenbergi give a version of this scold, with greater intra- than inter-individual variation displayed in the quality, pattern, frequency, and duration of scolds. Once an individual begins scolding/mobbing at regular intervals, however, scolds generally do not vary appreciably. Successive scolds of a single female (CBF No. 2629) soon after tape playback are

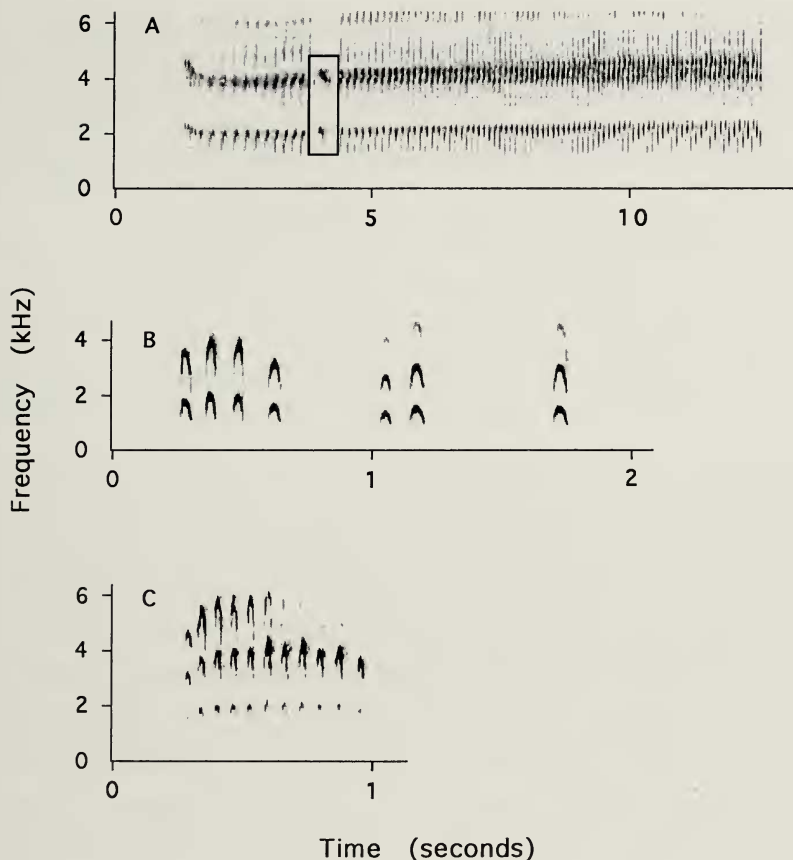


FIG. 6. Some vocalizations of *Scytalopus 'unicolor' parvirostris*. A. Adult (male ?), complete natural song. Cochabamba, Prov. Chapare, 3 km by road E Tablas Monte, 2615 m, 27 Feb 1992. Same song is given by central La Paz and Santa Cruz populations; differs from that of populations in northern La Paz and southern Peru. B. Age/sex unknown, scold/mobbing vocalization in which 1–4 syllable phrases are alternated randomly but delivered at regular intervals. Same loc., 2535 m, 27 Feb 1992. C. Adult (sex unknown), natural scold. La Paz, Prov. Nor Yungas, about 1 km S Chuspipata, 3000 m, 28 Mar 1993; CBF 2635.

shown in Fig. 3D and E. The latter illustrates the scold most typical of the species, which this female began giving consistently several sec after I ceased tape playback. I suspect that females give the scold more often than do males and that females' scolds are slightly higher-pitched than those of males, as reported by Fjeldså and Krabbe (1990:423) for the genus in general. Across the genus *Scytalopus*, there is much less variation in scolds than in songs (pers. obs.; compare Fig. 3D and E with

probably distantly related but sympatric taxa in Figs. 5C and 6C). This probably indicates that the vocalizations we have identified as songs are more important than scolds as reproductive isolating mechanisms. There may be selective pressure to maintain (or converge toward) interspecific similarity of scolds/mobbing vocalizations if such lack of variation leads to widespread recognition of the warning or alert message among sympatric species of birds, as suggested by Thorpe (1956).

Other distinctive vocalizations of *S. schulenbergi* include a single, piercing "peeyk!" and an alarm call consisting of one or two sharp introductory notes followed by several level, evenly spaced couplets of sharp syllables, then a few triplets, ending with a higher syllable or two, the whole bout lasting 2–5 sec ($N = 2$). This vocalization is given only once, immediately after a bird is startled, as opposed to repeatedly like the scold.

Systematic relationships.—Looking for relatives among Andean *Scytalopus*, the conspicuous white forehead of *schulenbergi* immediately brings to mind the Andean Tapaculo (*S. magellanicus*) of Southern Argentina and Chile. However, the two have very different songs (compare Fig. 3A–C with sonagram p. 437 of Fjeldså and Krabbe [1990]) and, more importantly, there exists a near-continuum of populations (some unnamed) northward to central Peru (approximately the upper Huallaga River valley) sharing a *magellanicus*-type song, most of them essentially isolated geographically, and all occurring primarily at and above treeline. The entire range of *schulenbergi* (which inhabits humid-temperate forest at and below treeline) is paralleled by one of these forms, "*simonsi*" (sensu Fjeldså and Krabbe 1990), which lacks a conspicuous white forehead and has dark barring or other pattern on the flanks and rectrices in all plumages. In light of these considerations, I do not believe that *S. schulenbergi* can be assigned to the *magellanicus* superspecies (as defined below).

Perhaps with the exception of the taxa in eastern Brazil, the Silver-fronted Tapaculo (*S. argentifrons*) of the mountains of Costa Rica and western Panama is the member of the genus most geographically remote from *S. schulenbergi*. The diademed adult male plumage (and to a lesser extent, the plumages of females and immatures) of *argentifrons* is, however, remarkably similar to that of *schulenbergi*. The basic pattern of the song of *argentifrons* (both subspecies) is also similar to that of *schulenbergi*, although it consistently begins more rapidly, and tends to rise slightly in frequency (Fig. 4A, compare with Fig. 3A and B). Scolds of the two species are also quite similar. It seems plausible that *argentifrons* and *schulenbergi* represent relicts at either end of an extraordinarily long, trans-Andean gap, although the gap could be occupied in part by taxa as

yet undiscovered. Such a relationship could easily be obscured, for example, if any extant, intervening relatives have lost the diadem or have not been tape-recorded. However, one intervening diademed population (only a small percentage of which have complete frontal bands) that has been tape-recorded, in western Depto. Pasco, Peru, is markedly different both by voice (a "chirping" note repeated at a short interval for long periods of time; Fjeldså and Krabbe 1990:440 and sonagrams pp. 437–442; [Fig. 4B, compare with Fig. 3A and B, Fig. 4A and C, and Fig. 5A]) and by habitat (above treeline in rocky shrub/grassland; G. and K. Rosenberg, pers. comm.). In both of these respects, the Pasco population appears to be most nearly allied to the *magellanicus* group. Although this distinctive population remains unnamed, it is almost certainly best treated as a species.

Particularly interesting is a series of four specimens taken within walking distance of a single camp at treeline in late July 1974 by T. A. Parker, III, D. A. Tallman, and G. Lester, 14 km NE of Abra Málaga along the road between Ollantaitambo and Quillabamba, Depto. Cuzco, Peru ("Canchaillo," 13°07'S, 72°22'W; Parker and O'Neill 1980). Habitat at this locality is heterogeneous, ranging from grassland with scattered rocks and shrubs to *Polylepis* woodland to dense, humid-temperate forest with abundant *Chusquea* spp. bamboo (Parker and O'Neill 1980). Two of the birds (LSUMNS No. 78578 [♂], 78581 [♀]) are very similar to *S. [m.] acutirostris* (this may actually be the appropriate name, but see comments below), and I suspect that they represent the *magellanicus* group occupying the grassland zone above treeline. One specimen's label gives the elevation as 13,000 ft (=about 3900 m) in *Polylepis* habitat, which, together with its plumage, places it almost certainly with the *magellanicus* group. The other specimen's label gives the elevation as "ca 10,700' " (=3240 m), which, lacking precise data on habitat, makes its assignment to the *magellanicus* group somewhat more ambiguous. The other two specimens (LSUMNS No. 78579[♂], 78580[♀]) are distinctly diademed and masked and are basically quite similar to *schulenbergi*; I believe these birds represent an unnamed population. One specimen's label gives the elevation as "ca 10,700'," and the other's label gives no elevation; neither provides any data on habitat. If the *magellanicus*-like bird is indeed in the *Polylepis*/grassland habitats above treeline, as I believe it must be, I suspect that the unnamed, diademed taxon from below Abra Málaga is to be looked for in the somewhat isolated humid-temperate forest of this region, perhaps especially near the local treeline. A recording of the terminal part of a song made by N. Krabbe at "St. Luis restaurant below Abra Málaga, 3000 m. in *Chusquea* bamboo" on 4 Dec. 1983 (a "sub-adult," not described, was collected and is at ZMUC [no catalog number

provided], N. Krabbe, pers. comm.), and another recording of the end of a song followed by scolds recorded by T. Schulenberg "below Abra Málaga, 3350 m . . . in edge of humid forest," 21 Jul. 1985 (no specimen collected, N. Krabbe, pers. comm.) sound much like vocalizations of *schulenbergi*. Without specimens or even detailed plumage descriptions for either of the birds recorded, however, I must stop short of attributing these recordings to the diademed Abra Málaga population, especially in light of the following considerations. The two Abra Málaga specimens, which have well-developed diadems and masks and are probably adults, show extensive brownish flanks with some dark barring on most feathers, and have short, brown tails (averaging 4 mm shorter than the tail of *schulenbergi*, Table 1) with conspicuous, alternating light and dark concentric bands on the rectrices, in all these respects differing noticeably from *schulenbergi*, especially adults. Considering the substantial geographic hiatus between Abra Málaga and Valcón in Depto. Puno and these documented plumage and mensural differences (albeit from a sample of only two from Abra Málaga), and lacking a complete and unambiguous sample of the voice, I feel that the Abra Málaga population cannot be definitely allied to *schulenbergi* at the present, although I suspect that it is, whether at the specific or subspecific level.

The two distinctive, unnamed populations discussed here have escaped description primarily because they inhabit remote regions that had not been collected sufficiently or at all when Zimmer turned his attentions to the genus in the late '30s. Apparently, Zimmer never saw a diademed *Scytalopus* from the Andes, and although he described several subspecies from northern and central Peru (Zimmer 1939), he introduced no names that could be applicable to either of the taxa under consideration.

More recent interest in naming distinctive populations of *Scytalopus* in central Peru has been stymied to some extent by confusion surrounding the applicability of the name *acutirostris*, first associated with the *magellanicus* group by Hellmayr (Cory and Hellmayr 1924:21), because the type locality is not definitely known, and the type specimen is difficult to assign to any particular population (T. Schulenberg and N. Krabbe, pers. comm.). Fjeldså and Krabbe (1990:443) suggested that "*acutirostris*" may represent the same form as *S. unicolor parvirostris*, but, perhaps more likely, the 'unnamed' species from c. Peru" (which they discuss on pp. 427–428), but provided no explanation for this novel treatment. Not having examined pertinent type specimens myself, I am nonetheless impressed that Hellmayr was so convinced of the similarity between *S. m. "simonsi"* (from Cochabamba, Bolivia) and *acutirostris* (although he was not comparing types, I believe he had selected appropriate material for this specific comparison, because he had previously examined and criti-

cally described the type specimen of *acutirostris*) that he stated, "a small series from w. Bolivia . . . is perfectly identical with two from Maraynioc which we may regard as topotypical of *acutirostris*" (Cory and Hellmayr 1924:22). This similarity applies to the intervening Abra Málaga population of the *magellanicus* group as mentioned above, and strongly suggests that the traditional treatment of *acutirostris* in this assemblage is appropriate. In the absence of compelling evidence to the contrary, then, the most conservative course is to regard *acutirostris* as the species-level name representing the *magellanicus* complex occurring from central Junín, Peru, southward to central Cochabamba, Bolivia. I can see no clear reason to recognize "*simonsi*" (sensu Fjeldså and Krabbe 1990) at even the subspecies level. I agree with Fjeldså and Krabbe (1990) that this stretch of the Andes (Junín to Cochabamba) is probably inhabited by two or more allospecies in the *magellanicus* superspecies, and the name *simonsi* may stand for the population described from Cochabamba (whatever its distributional limits may be), but species limits in the *magellanicus* complex require further work to establish (perhaps involving analysis of "ancient DNA" to match the type of *acutirostris* to another central Peruvian population). Whether or not the above views are accepted, it seems clear that the name *acutirostris* cannot be applied to *schulenbergi*, nor to the diademed populations of *Scytalopus* inhabiting western Depto. Pasco or the Abra Málaga region in Depto. Cuzco.

Aside from the above considerations, I wish to point out that the population I have assigned to *S. schulenbergi* from Puno, Peru, really cannot be so designated with 100% certainty, because its song has not been tape-recorded. A recording made by N. Krabbe (pers. comm.) of the scold of an unseen *Scytalopus* "in fairly low, humid second growth above (N) Sandia, Puno, 2800 m on 25 Dec. 1983" sounds much like that of *S. schulenbergi*, although 2800 m is well below the elevation of any other specimen or recording of *schulenbergi*, including the LSUMNS series from Puno. Were it not for our discovery that *schulenbergi* definitely occurs within about 50 km (Pelechuco, in Depto. Franz Tamayo) with no reasonable geographic barrier in the intervening territory, I would be reluctant to include it because of the geographically complex gap southward to the type locality that would otherwise have to be included within the range. The known distribution of *S. schulenbergi*, from southern Puno, Peru, to Cochabamba, Bolivia, is shared by some other temperate-zone birds, such as *Andigena cucullata*, *Cranioleuca albiceps*, and *Hemispingus calophrys*, and it may be that these are its true limits.

The Bolivian range of *S. schulenbergi* may be fragmented by one or two natural barriers in Depto. La Paz: the canyons of the Rio La Paz and the Rio Mapiri, both of which represent arid or semi-arid gaps in the

distribution of humid-temperate forest on the east slope of the Andes. The former separates subspecies of at least three suboscines syntopic (pers. obs.) with *S. schulenbergi*: Black-throated Thistletail (*Schizoeaca harterti*) (Remsen 1981), Light-crowned Spinetail (*Cranioleuca albiceps*) (Remsen 1984), and *Grallaria rufula*. The Rio Mapiri canyon appears to be the most likely barrier separating *Schizoeaca harterti* and *S. helleri*. Thus, further investigation within Bolivia, especially in Depto. Cochabamba, may reveal that *S. schulenbergi* comprises two or three subspecies.

Biochemical analysis using specimens of known elevation and habitat and with accompanying voice recordings, including *S. schulenbergi*, currently is underway at ZMUC by P. Arctander (J. Fjeldså, in litt.).

Conservation.—For the present, *S. schulenbergi* is probably not seriously threatened as humid-temperate forest between 3100 and 3400 m exists in undisturbed condition in several remote regions of its range. The type locality, however, has been altered significantly in the past two years by the activities of a gold-mining cooperative which has encouraged more than 500 people to settle in a formerly pristine, forested canyon there. Fortunately, the Bolivian government has established and is planning to designate some important reserves that will protect not only taxa with distributions largely within Bolivia, such as *S. schulenbergi*, but also genetic corridors for the many more taxa that extend significantly north or south of the country.

Distribution and vocalizations of other Bolivian Scytalopus, with comments on the magellanicus complex.—From central Depto. Cochabamba northward to the Peruvian border, four taxa of *Scytalopus* are found as one descends from rocky grassland above treeline to the upper tropical rain forest of the east slope, in the following sequence: [*m.*] *acutirostris*; *schulenbergi*; 'unicolor' *parvirostris*; and 'femoralis' *bolivianus*. These four taxa may be encountered within a 20 km drive along the road between Unduavi and Coroico in Depto. La Paz. The situation south of central Depto. Cochabamba is much simpler, with the depression of tree-line and lower rainfall significantly narrowing the elevational width of humid forest. In this region, the first two taxa above drop out, *S.* [*m.*] *superciliaris* appears (perhaps as far north as central Depto. Cochabamba; see below), continuing southward to Prov. Tucumán, Argentina, and *S.* 'unicolor' *parvirostris* reaches its southernmost point of occurrence in extreme western Depto. Santa Cruz in the isolated Serrania de Siberia (Remsen and T aylor 1989, pers. obs.). In lower subtropical and upper tropical forests, *S.* 'femoralis' *bolivianus* is reported in the literature as far south as Prov. Florida, Depto. Santa Cruz (Remsen et al. 1986), and it has been found recently in Depto. Chuquisaca by J. Fjeldså and S. Maijer (J. Fjeldså, pers. comm.). Thus, only *S.* [*m.*] *superciliaris zimmeri*

is known to inhabit most of the southern half of Bolivia, especially at upper elevations. Songs and habitats of all these forms, with the exception of *S. [m.] superciliaris*, are at least partially described and illustrated with sonagrams in Fjeldså and Krabbe (1990). I offer the following information to supplement their species accounts, with emphasis on *Scytalopus* taxa within Bolivia, concluding with comments on the *magellanicus* complex.

S. 'unicolor' parvirostris.—In Bolivia, this taxon inhabits well-developed humid montane forest and connected second-growth and bamboo between about 2000 and 3200 m. It overlaps *S. 'femoralis' bolivianus* at the lower end, between about 2000 and 2300 m (but see account of *bolivianus* below), and *S. schulenbergi* at the upper end, between about 2975 and 3100 m. A full song from Prov. Chapare, Cochabamba is shown in Fig. 6A. Birds to the south in Depto. Santa Cruz, and those to the north, near the type locality of *parvirostris* in Depto. La Paz, have songs essentially indistinguishable from those of Cochabamba birds (pers. obs.). The population inhabiting the Pelechuco region of Prov. Franz Tamayo, however, sings a markedly different song. Although I did not manage to tape record it, I believe this song, which is characterized by significantly longer inter-syllable interval and is of a distinctive quality, is represented by the partial sonagram labeled "*parvirostris* Vilcabamba mts. (song)" on p. 426 of Fjeldså and Krabbe (1990), who described some variation in songs within the latitudinal range they ascribe to *parvirostris* (p. 427). No songs of topotypical *parvirostris* were heard during two days in appropriate habitat at proper elevations. Playback experiments that I performed by presenting songs of topotypical *parvirostris* to the birds below Pelechuco elicited no response, but scolds of this taxon from Prov. Nor Yungas and of *S. schulenbergi* caused previously undetected individuals to vocalize, once with a song, and once with a scold. A single female was collected (CBF No. 2646), which differs from a single female from Prov. Nor Yungas (essentially topotypical *parvirostris*) in having slightly more brown in the upper back and nuchal region, and somewhat less rufous-brown in the flanks (differences that I suspect comparison of series would show to be inconsistent). I was not able to perform reverse playback experiments. These two distinct song types apparently replace each other somewhere in northern Bolivia, perhaps across the Rio Mapiri. Further elucidation of this interesting situation awaits more field and biochemical work.

Two types of repetitive scold/mobbing vocalizations are illustrated in Fig. 6B and C. These are given by individuals from central La Paz southward at least to Santa Cruz. Both seem to stimulate other birds to scold as well. I do not know the difference in context in which these scolds are

given, except that I have noted that the scold in Fig. 6C seems to be given more frequently in response to the presence of an observer.

S. 'femoralis' bolivianus.—This little-known taxon primarily inhabits the interior of tall forest, favoring ravines and dark tangles at the edge of light gaps. It is frequently heard in the dense, herbaceous vegetation along roads in generally forested regions, mostly between about 1100 and 2300 m (pers. obs.). *S. 'femoralis' bolivianus* has an extensive vocal repertoire, including variation in inter-syllable interval of the songs given by a single individual (particularly apparent following tape playback). Part of a typical song, which does not include the beginning, is shown in the sonagram on p. 431 of Fjeldså and Krabbe (1990). The scold consists of fewer syllables than the scolds of other Bolivian *Scytalopus*, but is structured similarly. I have one anomalous record of an individual that I heard singing at the remarkably high elevation of 2850 m below Pelechuco in Prov. Franz Tamayo. Elsewhere in the northern half of Bolivia, only '*unicolor' parvirostris*' is known to occur at this elevation. In the Pelechuco region, however, true *parvirostris* appears to be replaced by another taxon (see above). Further investigation could show this taxon to have a somewhat different elevational distribution, or perhaps '*femoralis' bolivianus*' truly occupies a wider elevational range in this part of Bolivia.

S. [m.] superciliaris.—A typical section of the long song of *superciliaris*, in which it delivers a labored series of conspicuously bisyllabic notes in the pattern of nominate *magellanicus* to the south (see sonagram p. 437 of Fjeldså and Krabbe 1990), and *[m.] acutirostris* to the north (Fig. 5A), is shown in Fig. 4C. Nominate *superciliaris* lives in a wide variety of habitats, from dry, rocky ravines well above treeline where the dominant vegetation is *Festuca* sp. grass to rocky ravines and talus slopes in the much more humid *Alnus* and "yungas" forests as low as about 1400 m (pers. obs.). The subspecies *zimmeri*, known to occur only in Deptos. Chuquisaca and Tarija, "sounds like a *superciliaris*, but has the stress on first instead of second syllable" (recording by J Fjeldså, N. Krabbe, pers. comm.). Both by voice and by plumage, N. Krabbe (pers. comm.) considers *zimmeri* to be intermediate between nominate *superciliaris* to the south and "*simonsi*" to the north, and favors merging the three forms under *superciliaris* (the oldest name).

A female (LSUMNS 37781) collected by Steinbach in October 1937 at Colomi in the mountains of central Cochabamba (17°21'S, 65°52'W, 3800 m; Paynter 1992) may represent an intergrade between *zimmeri* and *acutirostris*/*"simonsi"*. It has a distinct white superciliary narrowly crossing the forehead, and thick, dark bars on the rump, flanks, tail coverts, and tail. The throat is slightly paler gray than the breast. Two additional intergrades were collected in 1987 at "Khasa Punta Pampa near Rodeo

W of Vacas, Cochabamba (DNA analyzed)" (J. Fjeldså, pers. comm.). That *zimmeri* and *acutirostris*/*"simonsi"* might hybridize is not surprising given the lack of an obvious geographic barrier, the fact that they at least partially share the same habitat, and the relatively close similarity in their songs. I expect that these two or other "species" of *Scytalopus* occasionally interbreed, because many populations of *Scytalopus* (named or not) are in direct contact with at least one other morphologically similar population, and this circumstance is compounded by the crowding effect resulting from human alteration of natural habitats: different vocalizations and habitats may not always ensure reproductive isolation. The lack of external structural and plumage differentiation across the genus must also make it very difficult or impossible for researchers to recognize a hybrid individual in the vast majority of instances. However, under those relatively rare circumstances in which one finds two vocally and morphologically similar but separable populations in geographical proximity, such as the *magellanicus* form in central Cochabamba (whether correctly called *acutirostris* or *"simonsi"*) and *superciliaris zimmeri*, recognition of a hybrid should be comparatively easy.

S. [m.] acutirostris.—This taxon (which may properly be known as *simonsi*; see above) inhabits rocky shrub/grassland above natural treeline. It has a rather extensive vocal repertoire, including several characteristic one- and two-note vocalizations that appear to function as alarm or pair contact calls, and several vocalizations given mostly in response to tape playback. After the song (Fig. 5A), the most commonly heard vocalization is a descending, slightly accelerating series of "weenk" notes delivered slowly enough to be counted easily (Fig. 5B). Similar kinds of vocalizations are given by the huge *Pteroptochos* tapaculos in Chile (pers. obs.). This vocalization is certainly given by females (CBF No. 2642), often while the male is singing, and it may be given by males as well. In any event, it is delivered only once, and at irregular intervals. The scold in Depto. La Paz is shown in Fig. 5C. I am perplexed by the fact that I have not heard this scold (or any "substitute" scold) from birds in Depto. Cochabamba, although I have encountered many individuals in several localities there.

The "*magellanicus* group/complex," first defined in Zimmer's (1939) strictly morphological classification, comprises "the smallest and at the same time elevationally highest-ranging members of the genus," including taxa from northwestern Venezuela south to Tierra del Fuego and the Cape Horn Archipelago (Fjeldså and Krabbe 1990:437–443). These many forms are currently treated (with the single exception of *superciliaris*) either as a single species with numerous subspecies (Sibley and Monroe 1990) or as allospecies of a single superspecies (Fjeldså and Krabbe 1990:

437). There is, however, a clear break in song-types and, to a lesser extent, habitats, within this assemblage at the "North Peruvian Low" (defined by Vuilleumier 1984) in Depto. Cajamarca, northwestern Peru (pers. obs.). Populations to the south of this barrier have songs that are a long series (occasionally in excess of 3 min) of steadily cadenced, monosyllabic or bisyllabic notes (these occur from approximately the upper Huallaga River valley southward to Cape Horn; Fjeldså and Krabbe 1990, sonagrams pp. 437, 439, 440, top of 441; pers. obs.). In a few forms this pattern is varied to a long series of short, burry notes (Fjeldså and Krabbe 1990, sonagrams pp. 437, bottom of 441, and top of 442; pers. obs.). Populations to the north of the North Peruvian Low for which voices are known have songs that consist of a single, vibrating trill several seconds long (perhaps averaging 10–15 sec), in which individual syllables are delivered at a rate of more than 30/sec, and which, in the taxon *griseicollis*, often begin with 1–3 short stutters, then continue without interruption, slowing slightly toward the end (pers. obs.). There are two anomalies to this scenario: Hilty and Brown (1986:429) attributed a vocalization transcribed as "a measured ser. of double whistles, ty-ook, ty-ook, ty-ook . . ." to *S. 'magellanicus' canus* in Depto. Nariño, Colombia, and Fjeldså and Krabbe (1990:442) suggested that birds from Cerro Chinguela, Depto. Piura (north of the North Peruvian Low), may represent *S. [m.] affinis*, which otherwise occurs only to the south of the North Peruvian Low, and which sings a southern song type (sonagram p. 442). N. Krabbe considers the song of *canus* unknown (pers. comm., contra Fjeldså and Krabbe 1990:443), and my field experience indicates that the "*magellanicus*" population high on Cerro Chinguela sings a northern song type, which is apparently the same as that of *S. 'magellanicus' opacus* of Ecuador, the nearest form to the north. Additionally, it seems that northern populations tend to favor woody vegetation and bamboo along the forest/páramo ecotone more than the relatively open, rocky shrub/grassland inhabited by most of the southern populations. Therefore, I recommend that the *magellanicus* complex be reorganized to allow these two high-altitude, geographically isolated, vocally distinct groups to stand on their own as superspecies, maintaining the name *magellanicus* for populations south of the North Peruvian Low that are vocally and genetically determined to be allied to nominate *magellanicus* (I suspect that there is more than one group within the southern assemblage) and establishing the name *griseicollis* for vocally and genetically related populations north of the North Peruvian Low. Inherent in this reorganization is the reinstatement of *griseicollis* to species status. Species limits within these superspecies, and the degree of relatedness of the two superspecies themselves, will require

further field and laboratory work to determine and, in any case, are beyond the scope of this paper.

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COLOR PLATE

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